

Perch (*Perca fluviatilis*) as a factor in recruitment variations of vendace (*Coregonus albula*) in lake Konnevesi, Finland

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Received 15 Nov. 2002, revised version received 25 June 2003, accepted 11 July 2003

Valkeajärvi, P. & Marjomäki, T. J. 2004: Perch (*Perca fluviatilis*) as a factor in recruitment variations of vendace (*Coregonus albula*) in lake Konnevesi, Finland. — *Ann. Zool. Fennici* 41: 329–338.

The population dynamics, especially recruitment, of vendace (*Coregonus albula*) in lake Konnevesi were analysed from a time series of three decades from 1971 onwards. Recruitment success was highly variable, with no clear relationship between spawning stock and recruitment. Furthermore, no regular recruitment failure from large spawning stocks that would imply over-compensation was detected. Since 1982, an 11-year period of very poor year classes occurred despite the spawning stock and larval density being at high enough levels to produce abundant year-classes in the beginning of this period. A comprehensive recession appeared at the same time in other vendace stocks in southern Finland. In lake Konnevesi, perch (*Perca fluviatilis*) stock increased rapidly during the vendace recession. High summer temperatures were revealed to strengthen the perch stock, especially in the 1980s, as indicated by CPUE data with a lag of two years. Perch probably delayed the recovery of vendace and it is also likely that its predation affected the dynamics of the vendace stock even in the beginning of the recession. We suggest that predation pressure as a whole was an important factor for the onset and duration of the vendace recession.

Introduction

Vendace (*Coregonus albula*) is the most important target species for commercial fishermen and is also the desired catch for recreational fishers in Finnish inland waters. However, strong year-class fluctuations are a major problem for such vendace fisheries and several abiotic and biotic hypotheses have been proposed as to the possible reasons for these fluctuations (e.g. Järvi 1942, Viljanen 1986, Salojärvi 1987, Heikinheimo 2001).

Factors affecting vendace recruitment, including the spawning stock–recruitment (S–R) relationship, probably hold the key for understanding stock fluctuations in this species. Weather conditions during the spawning and larval period as a crucial factor were pointed out by Järvi (1942) and good recruitment has been related to high temperature in the spring (Helminen & Sarvala 1994). Some authors (Aass 1972, Viljanen 1988) did not find any connection between the abundance of spawners and recruits, while others (Valtonen & Marjomäki

1988, Salojärvi 1991, Marjomäki 2003) suggested a compensatory relationship. Myers and Barrowman (1996) concluded that generally high recruitment needs high spawning stock and Karjalainen *et al.* (2000) regarded high larval number to be necessary for the high recruitment of vendace. Viljanen (1988) proved that the number of spawners correlates only with egg and larval abundances, and not with recruits. However, the relationship between the abundance of a late-post larval stage and subsequent year-class strength was strong.

When considering stock fluctuations, a distinction has to be made between short-term and long-term variations. In the short-term case, a rather regular occurrence of strong year class 2–3 years apart is typical in many lakes (e.g. Sandlund *et al.* 1991, Helminen & Sarvala 1994, Auvinen *et al.* 2000, Karjalainen *et al.* 2000). Several intraspecific factors such as asymmetric food competition (Aass 1972, Hamrin & Persson 1986, Auvinen 1988, Helminen & Sarvala 1994, Huusko 1998, Auvinen *et al.* 2000) and egg and larval quality (Sarvala & Helminen 1995) have been suggested as reasons for such oscillations.

Sometimes recruitment may fail for as long as a decade. Examples are during the 1930s in lake Keitele (Järvi 1942) and from the mid-1980s to the mid-1990s in many lakes of southern Finland (Valkeajärvi *et al.* 2002). The reasons behind these long-term variations are not clear but changes in predation pressure caused by perch (*Perca fluviatilis*) and brown trout (*Salmo trutta m. lacustris*) have been suggested as a potential factor (Helminen & Sarvala 1994, Valkeajärvi & Bagge 1995, Valkeajärvi *et al.* 1997, Heikinheimo 2001). Synchrony within close geographical regions seems to be typical of both short-term and long-term variations (Valkeajärvi *et al.* 2002, Marjomäki *et al.* 2004) and is suggested to be due to spatially correlated environmental stochasticity, e.g. weather conditions, after hatching either directly or through synchrony in predatory populations (Marjomäki *et al.* 2004).

The aims of this study were to analyse three decades of population dynamics data for lake Konnevesi vendace in order to determine the significance of density dependent, biotic and abiotic factors for vendace recruitment. The main emphasis was on the interactions between vendace and perch.

Material and methods

The study was conducted in the southern basin of lake Konnevesi (area 119.5 km²), an oligotrophic lake in central Finland (62°40'N, 26°30'E). Mean depth of the lake is 12.5 m and maximum depth 56 m. The lake is thermally stratified with a thermocline situated at 10–15 m depth in summer (Tuunainen 1972).

The fish stock of lake Konnevesi has been monitored since 1970. Up to 1977 the monitoring was based on catch per unit effort of test fishing gill net series (CPUE, kg per series per day) consisting of 10, 12, 14, 17 and 21 mm gill nets from knot to knot (2.1 m by 30 m). The test fishing was carried out at intervals of two weeks from May to October and the gill nets were set in fixed monitoring sites in the pelagic zone at a depth of 7–9 m. About 90% of vendace and perch catch were caught from July onwards (Puttonen & Valkeajärvi 2000, P. Valkeajärvi unpubl. data).

Since 1978, CPUE (kg) of seine (12 by 180 m, mesh size in a cod-end 8–10 mm) and gill nets (3 by 30 m, mesh size 14–18 mm from knot to knot) in normal vendace fishing activities were used for monitoring. Fishermen (10–15 individuals) kept a record of their catches (kg) and efforts (seine hauls per day, gill net days) around the year but only the data of July–October were used for stock monitoring (Valkeajärvi 1995, Valkeajärvi & Bagge 1995). In 1980, 1981, 1982, 1991 and 1996, a gill net series was used simultaneously with normal vendace gill netting to inter-calibrate the methods. The catches of test fishing gill nets were standardized with normal vendace gill nets by means of net area before calculating regressions between the catches.

The total CPUE of gill nets (kg) in normal fishing was used as the index of spawning stock biomass (gill net catches includes only mature vendace). The spawner index from 1971 to 1977 consisted of the CPUE of test fishing. This was calibrated against an index from normal gill netting by means of regression between the CPUE of 12–17 mm gill nets in test fishing and the CPUE in normal fishing in comparison years as mentioned above ($r^2 = 0.95$, $n = 5$).

The CPUE (individuals in gill nets) of one-year-old (1+) vendace was used as the relative index of recruitment (0+) of the previous year.

Because of scarce seining in numerous years, only more size-selective gill net data were available for such analyses (see Valkeajärvi & Bagge 1995). Because the test fishing data contained no material for ageing, an indirect method was used to estimate the recruitment index from 1971 to 1977 based on a linear regression between the CPUE (individuals) of 10 mm gill nets (test fishing) with a lag of one year and the recruitment index estimated from CPUE of normal fishing (see above and Valkeajärvi 1995) in the comparison years ($r^2 = 0.90$, $n = 5$).

Since 1978, CPUE (kg) in small mesh (14–18 mm) gillnets (normal fishing) was used as an index of perch stock. Also, the CPUE (kg) data of seine and of large mesh (27–33 mm) gill nets were used for estimating size distribution of the perch stock. From 1971 to 1977, the perch index was calculated by means of regression between the CPUE of 10–17 mm gill nets (test fishing) and the CPUE in normal fishing of the comparison years ($r^2 = 0.44$, $n = 5$).

Vendace catch samples (mean 240 individuals per year) were taken in the autumn of each year. In the beginning of the monitoring the age distribution of vendace was based on seine samples, but since 1984 samples have to be taken from gill nets because of reduced seining. One-summer-old vendace were excluded from seine catches to calibrate the age distribution with gill net samples. Scales were used for age determination.

Larval sampling was carried out with a shore bag seine (mesh size one mm) from 1984 to 2000 at 13 fixed sites in the littoral area around the lake. The samples were collected in May about one week after ice-off and three hauls were made at each site (about 100 m² per haul) (Valkeajärvi & Bagge 1995).

The statistical analysis was started by removing the effect of the spawning stock biomass on recruitment by fitting each of the following spawning stock-recruitment models:

$$\begin{aligned} \text{Proportional} & R_t = \alpha S_{t-1}, \alpha > 0 \\ \text{Cushing (1971)} & R_t = \alpha S_{t-1}^\gamma, \alpha, \gamma > 0 \\ \text{Ricker (1954)} & R_t = \alpha S_{t-1} \exp(-\beta S_{t-1}), \alpha, \beta > 0 \end{aligned}$$

where R_t = index of number of one-summer-old (0+) recruits in autumn t , S_{t-1} = index of spawning stock biomass in autumn $t - 1$, and α , β and

γ = model parameters. The parameters were estimated for ln-transformed models by iterative least squares. Thus, the random component ε was assumed to be log-normally distributed (e.g. Peterman 1981, Hilborn & Walters 1992), i.e.

$$\ln R_t = \ln(f(S_{t-1})) + \varepsilon, \varepsilon \sim N(0, \delta^2).$$

Performance of the nested models (one model being a special case of another in the sense that it can be obtained by special settings of one or more parameters) was compared using F -test (e.g. Iles 1994). The model residuals were calculated by

$$\text{Res}_t = (\text{observed } \ln R_t - \text{expected } \ln R_t).$$

In order to reveal non-stationarity of parameters, the time-series dependence of model residuals was analysed as suggested by Walters (1987).

The effects of other variables on recruitment were analysed by determining Spearman rank order correlations between the variables and recruitment model residuals. Spearman correlation was used because the effect could not be assumed to be linear for all the variables. In case of significant correlation and linear appearance of the variable-residual plot, the variable (V_i) was included in the S-R model assuming multiplicity of the effects

$$\ln R_t = \ln(f(S_{t-1})) + \theta_i(V_i - \text{mean}(V_i)) + \varepsilon, \varepsilon \sim N(0, \delta^2).$$

The variables analysed were:

Intra-specific

Previous year recruitment

Other biotic

CPUE of perch in seine (kg)

CPUE of perch in small mesh

(14–18 mm from knot to knot) gillnets

CPUE of perch in large mesh (27–33 mm from knot to knot) gill nets

Abiotic environmental factors affecting vendace larvae:

Time of ice break-up (Julian date)

Mean air temperature during four weeks after ice break

Sum of squared wind measurements during four weeks after ice break.

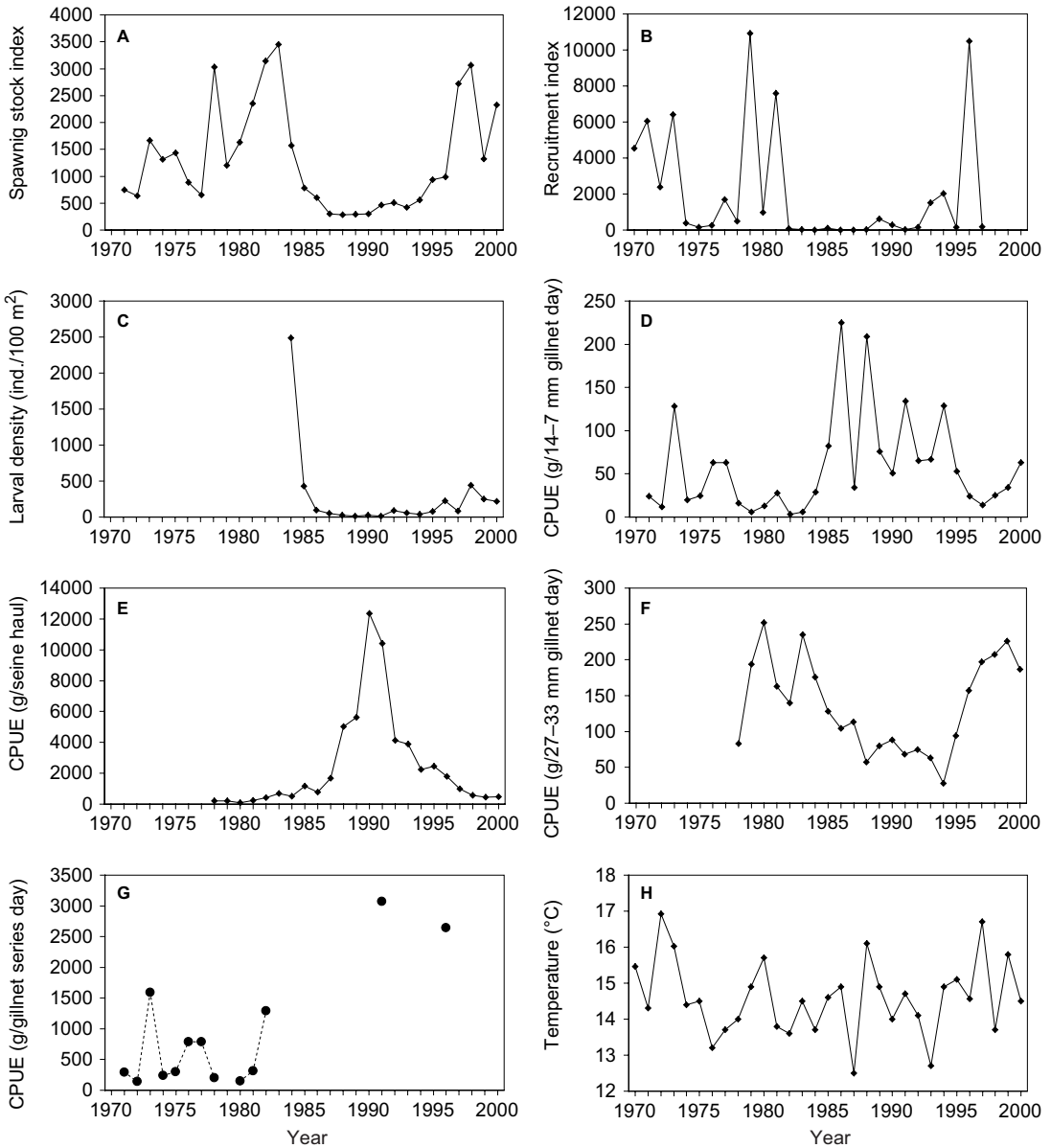


Fig. 1. The most important time series analyzed from 1971 to 2000. — **A:** index of vendace spawning stock. — **B:** index of vendace recruits. — **C:** vendace larval density one week after ice-off. — **D:** index of small perch (CPUE (g) of perch in 14–17 mm gill nets from knot to knot). — **E:** CPUE (g) of perch in seine. — **F:** index of big perch (CPUE (g) of perch in 27–33 mm gill nets). — **G:** CPUE of perch in test fishing (g per gill net series day) (Puttonen & Valkeajärvi 2000). — **H:** mean temperature from June to August.

The perch variables were cross-correlated with residuals relating Res_t to CPUE indexes of perch in years t , $t + 1$ and $t + 2$ because it was suspected that perch CPUE based on fishers' catch records is a delayed index of effective perch stock (*see* further details in discussion).

Data on ice break-up dates were collected by the Finnish Environment Institute and those of air temperature and wind were taken by the Finnish Meteorological Institute at a nearby airport (50 km). The wind measurements were squared because it was assumed that wind energy

is proportional to squared velocity. Squaring also served to emphasize the effect of occasional storms on the data.

Results

In lake Konnevesi, an 11-year period of very poor year-classes (from 1982 to 1992) was distinctive within the monitored period from 1971 to 2000 (Fig. 1). In addition, a three-year period of weak year-classes occurred in the mid 1970s. The recovery of the stock from the most recent collapse started gradually in 1993, and was completed by the year-class of 1996. Excluding the recession period, there seemed to be a tendency for a two-years cycle.

After the vendace collapse, the index of perch stock increased rapidly in small mesh gill net catches and gradually also in the seine catch (Fig. 1). During the recession of vendace recruitment from 1982 to 1992 the mean CPUE of perch was 3.5-fold greater in seine (3891 g/haul) and 2-fold greater in small mesh gill nets (83 g per gill net) as compared with the mean of other years. A significant negative Spearman correlation was found between the CPUE of vendace and small perch both in seine ($r_s = -0.771$, $p < 0.001$) and in gill nets ($r_s = -0.705$, $p < 0.001$). The index of big perch (the CPUE of 27–33 mm gill nets) correlated positively with vendace in gill nets ($r_s = 0.725$, $p < 0.001$), but negatively with small perch (the CPUE of 14–18 mm gill nets) ($r_s = -0.709$, $p < 0.001$).

The S–R relationship of vendace was obscure (Fig. 2), even though the smallest spawning stocks typically produced weak year-classes. The lowest index of spawning stock producing an abundant year-class was over 600 g/3 m by 30 m gill net. No regular recruitment failure from large spawning stocks that would imply over-compensation was detected and large spawning stocks produced both large and small year-classes. The Cushing and Ricker S–R models fitted the data better, but not significantly so, than the model of constant proportionality (Tables 1 and 2). Non-stationarity of S–R-model parameters was evident based on autocorrelation analysis (Fig. 3) and the very low level of recruitment, despite the presence of ample spawning stock since 1982.

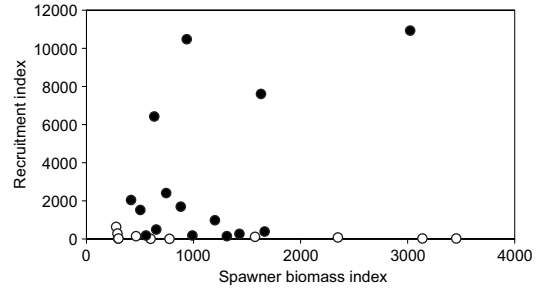


Fig. 2. Relationship between vendace spawning biomass and recruitment. The open circles represent the vendace recession period from 1982 to 1992.

The residuals of all the S–R models correlated significantly with the CPUE of perch in small mesh gill nets two years later (all Spearman $r_s < -0.53$, all $p < 0.004$, 1-tailed). Inclusion of this index in the models improved the fit significantly (Tables 1 and 2). No significant auto-correlations that would imply non-stationarity were found in the residuals of the models after the inclusion of the perch index. The distribution of residuals did not differ from normal (Kolmogorov-Smirnov test: all $p > 0.84$, 2-tailed). The other analysed variables showed no significant association with the residuals (all $p > 0.10$).

During 1984 to 2000, the larval density of vendace varied greatly (Fig. 1) with a mean density of larval vendace of 272 ind. per 100 m² (SD = 587 ind. per 100 m², range from 14 to 2489 ind. per 100 m²). In the deepest recession (1986 to 1992), the density was 45 ind. per 100 m² (SD = 35 ind. per 100 m², range from 14 to 93 ind. per 100 m²). The newly-hatched larval density correlated significantly with the spawning stock ($r_s = 0.936$, $p < 0.001$, all data) (Fig. 4). This correlation was also found during the vendace recession ($r_s = 0.851$, $p = 0.003$, $n = 9$). However, there was no correlation between the larval density one week after ice-off and recruitment ($p > 0.10$).

Discussion

In lake Konnevesi, vendace stock fluctuated drastically during the monitored period from 1971 to 2000. Two different levels in abundance of the vendace stock were found. Firstly, a short-term oscillation typical of many vendace stocks

in Finland (Viljanen 1986), and secondly a long recession from the mid 1980s to the mid 1990s. In addition, a short collapse was also present from 1974 to 1976.

In lake Konnevesi, the observed vendace stock fluctuations during the high stock period include signs of a two-year cycle implying density-dependent regulation as in many other lakes (e.g. Helminen & Sarvala 1994, Auvinen *et al.* 2000). The lack of a statistically significant effect of the strength of previous year-classes

on recruitment success may be due to the low number of abundant year-classes during the period studied. Effective fishing plays an important role in maintaining a two-year cycle in vendace recruitment (Auvinen 1994, Karjalainen *et al.* 2000) and Salojärvi (1987) suggested that the composition of the fish assemblage together with fishing levels determine the level at which the vendace population fluctuates. In lake Konnevesi, fishing effort has been rather low inducing no essential effects on the vendace stock.

Table 1. Estimated parameters of vendace spawning biomass (SB)–recruitment (R) functions. RSS = residual sum of squares, df = degrees of freedom, S.E. = standard error of estimate, r^2 = coefficient of determination, ar^2 = adjusted coefficient of determination, Perch_{t+2} = the CPUE of perch in small mesh gill nets two years after vendace recruitment, C.L. = confidence limit of coefficient.

Model	Equation	RSS	df	S.E.	$r^2\%$	$ar^2\%$
Proportional upper 95% C.L. lower 95% C.L.	$\ln R_t = -1.20 + \ln S_{t-1}$ -0.17 -2.2	160.8	25	2.54	< 1	< 1
Cushing upper 95% C.L. lower 95% C.L.	$\ln R_t = 5.3 + 0.036 \ln S_{t-1}$ 15 1.4 -3.9 -1.3	147.5	24	2.48	< 1	< 1
Ricker upper 95% C.L. lower 95% C.L.	$\ln R_t = -0.027 + \ln S_{t-1} - 0.0010 S_{t-1}$ 1.6 0.00008 -1.6 -0.0021	139.4	24	2.41	5.4	5.0
Proportional + Perch_{t+2} upper 95% C.L. lower 95% C.L.	$\ln R_t = -1.2 + \ln S_{t-1} - 0.024(\text{Perch}_{t+2} - 57.3)$ -0.33 -0.0092 -2.1 -0.040	110.2	24	2.14	25	23
Cushing + Perch_{t+2} upper 95% C.L. lower 95% C.L.	$\ln R_t = 5.1 + 0.071 \ln S_{t-1} - 0.024(\text{Perch}_{t+2} - 57.3)$ 13 1.2 -0.0096 -2.6 -1.1 -0.039	97.8	23	2.06	34	30
Ricker + Perch_{t+2} upper 95% C.L. lower 95% C.L.	$\ln R_t = -0.32 + \ln S_{t-1} - 0.00075 S_{t-1} - 0.022(\text{Perch}_{t+2} - 57.3)$ 1.06 0.00020 -0.0073 -1.71 -0.0017 -0.037	98.7	23	2.07	33	29

Table 2. Comparison of nested models in Table 1 by F -test. RSS = residual sum of squares, Perch_{t+2} = the CPUE of perch in small mesh gill nets two years after vendace recruitment.

Models compared	Reduction in RSS	F	p
Proportional vs. Cushing	13.3	2.07	0.16
Proportional vs. Ricker	21.4	3.32	0.08
Proportional vs. Proportional & Perch_{t+2}	50.6	7.86	< 0.01
Cushing vs. Cushing & Perch_{t+2}	49.6	8.08	< 0.01
Ricker vs. Ricker & Perch_{t+2}	40.7	7.01	0.01

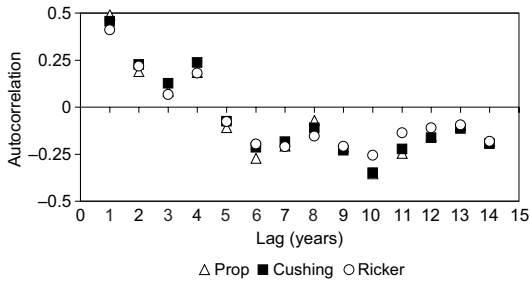


Fig. 3. Autocorrelation of residuals for proportional (Prop), Cushing and Ricker S–R models for lake Konnevesi vendace.

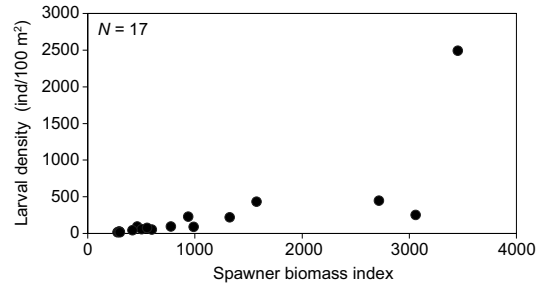


Fig. 4. Relationship between vendace spawning biomass and the newly hatched larval density in mid May one week after ice-off.

Dependence of larval density on spawning stock abundance agrees with observations of other authors, as does the low correlation between larval density one week after ice-off and recruitment (e.g. Viljanen 1988, Auvinen *et al.* 2000). Specific to lake Konnevesi, low larval abundance forecasts poor recruitment and a high number is needed to produce a large number of recruits, without a guarantee of strong recruitment as in many other lakes (Karjalainen *et al.* 2000).

Low larval density, poor spawning stock and high perch abundance were characteristics of the vendace recession period in lake Konnevesi. In addition, increased growth of vendace was previously documented as a feature of the collapse as a result of weakened food competition (Valkeajärvi & Bagge 1995). A crucial question is which reasons initially triggered the long recession of vendace in the mid 1980s, because until 1984 both the spawning stock and larval density one week after ice-off were still abundant enough to produce strong year-classes.

Perch and vendace have alternated as the most abundant species in lake Konnevesi on the basis of test fishing (Puttonen & Valkeajärvi 2000). Predation of perch on vendace larvae has been documented by Huusko and Sutela (1992) and two-year-old (100 mm) perch may consume vendace larvae during some weeks after ice-off. In lake Konnevesi, Tolonen (2000) found predation by larger perch to continue throughout the first summer of vendace life, but in lake Puruvesi only perch of 146 mm and greater were found to eat young vendace (Jaatinen *et al.* 1999).

We believe that during 1982 to 1984 perch was more abundant than indicated by the CPUE

data of normal fishing. This conclusion is supported by results of test fishing by gill nets 10–17 mm (Puttonen & Valkeajärvi 2000), where an almost nine-fold increase in the perch CPUE (kg) was recorded in 1982 as compared with 1980. In the normal vendace gill netting (14–17 mm), the increase in perch was not found clearly until 1985. Thus normal vendace gill nets, set to catch adult vendace and avoid small perch, indicate perch year-class strength with a longer time lag than do small mesh test fishing series. Furthermore the test fishing series, which were situated closer to shoreline caught younger perch than did normal vendace gill nets mostly set further from the shore. In addition, it is possible that fishers' book-keeping did not pay attention to perch catch enough owing to its by-catch role when the vendace catch was abundant.

Many studies have demonstrated that the recruitment of perch benefits from warm summers (e.g. Böhling *et al.* 1991, Mills & Hurley 1990, Karås 1996). Lappalainen *et al.* (1996) suggested that temperature is directly or indirectly the main reason for the variations in year-class strength of perch. Helminen and Sarvala (1994) applied this knowledge using the abundance of two-year-old perch (temperature sum of summer with a lag of two years) as an index of predator pressure on vendace larvae. They suggested that in Pyhäjärvi the abundance of predators and the warming of the water after hatching of larvae in spring together determine the final year-class strength of vendace.

Summer temperature also plays a great role in lake Konnevesi in the fluctuations of the perch stock. After the exceptionally warm

summers of 1972 and 1973, a short collapse in vendace recruitment followed during the period from 1974 to 1976 and after the warm summer of 1980, the long recession started in 1982 to 1983. In addition, in 1988 the high temperature was probably beneficial for perch reproduction, which would explain the increase in the perch CPUE observed in seine catches two years later and leading to prolonging of the vendace recession. In lake Konnevesi and most other Finnish vendace lakes, the water column is strongly stratified, reducing the likelihood of the alternative explanation that mortality of young vendace is caused by too high surface temperatures.

A conspicuous feature in the perch stock was an alternation of small and big fish based on the CPUE of small and large-meshed gill nets. Density of big perch (the CPUE in 27–33 mm gill nets) was highest during the period of strong vendace stock, while that of small perch was strongest during the vendace recession. In 1979, 1981 and in the end of 1990s big perch did not prevent the increase in vendace in spite of high CPUE. It is most probable that small perch is a greater threat to vendace than big perch because of its greater abundance. Even if the CPUEs of small and big perch have been similar in terms of biomass, small perch have been mostly from five to ten-fold greater in numbers (Puttonen & Valkeajärvi 2000). It is well known that food consumption of small fish is greater than that of big fish per weight unit (e.g. Brett & Groves 1979, Karås & Thoresson 1992).

Cannibalism plays an essential role in perch dynamics (e.g. Alm 1952, LeCren 1987, 1992) and the opposing trends in CPUE of perch in small and large mesh gill nets may also relate to differences in recruitment, to a possible variation in rate of cannibalism. Wahlström *et al.* (2000) suggested that big perch are able to keep the number of young perch low and according to Sanderson *et al.* (1999), long-term cycles of yellow perch (*Perca flavescens*) are generated by intraspecific interactions. Perhaps partly for this reason, big and small perch have not been numerous in lake Konnevesi at the same time. When the increase of big perch started, the number of small perch decreased rapidly in spite of warm summers. Presumably cannibalism plays occasionally an essential role in the varia-

tions of the perch stock in lake Konnevesi, with variable consequences for the vendace population.

The large-scale recession of vendace in the whole of southern Finland since the mid 1980s (Valkeajärvi *et al.* 2002) suggests a common cause. Could predation and especially perch predation on larvae and young vendace produce such prolonged recession? Synchrony between neighbouring lakes in the inter-annual variation of vendace recruitment seems to be related to environmental forcing, possibly through weather conditions directly regulating vendace recruitment, but perhaps also indirectly through the dynamics of their most important predators (Marjomäki *et al.* 2004). Increase of perch during the vendace recession after the mid 1980s was documented in lake Päijänne (Heikinheimo *et al.* 2002) and in Pyhäjärvi (Sarvala & Helminen 1996). Lappalainen *et al.* (1996) found that covariations in year-class strength were similar between populations of perch in the Finnish coastal waters of the Baltic Sea when they were separated by less than 300 km. In addition, Böhling *et al.* (1991) found similar variations in year-class strength of perch populations on the same side of the Baltic Sea.

The scientific documentation of the vendace recession of the 1980s is not unique. In the 1930s, vendace recruitment failed in lake Keitele for at least eight years (Järvi 1942). According to the Finnish Meteorological Institute (A. Nordlund pers. comm.), the summers of this decade were the warmest in the whole century in Finland, which agrees with the present hypothesis that relationships between temperature, perch and vendace exist.

In addition to the above considerations, the effect of brown trout predation on vendace has been found to be significant when stockings have been abundant (Valkeajärvi *et al.* 1997, Salonen 1998). In the 1980s, stockings of brown trout increased in Finland for ten consecutive years (Finnish Fishery Time Series 2001). However, Heikinheimo (2001) in her model examination, suggested the role of perch to be more important for vendace than that of brown trout.

In conclusion, it is very probable that predation pressure as a whole was crucial for the decade-long vendace recession in lake Konne-

vesi and in the whole of southern Finland at the same time. We agree with the opinion of Karjalainen *et al.* (2000) who emphasized the need for knowledge on food availability and predation in vendace lakes. Detection and understanding of the relationship between vendace and perch predation requires long-term monitoring of perch stock abundance together with studies of its feeding ecology.

Acknowledgements

We thank over ten fishermen for their book-keeping, catch samples and taking part in test fishings, Mr. Markku Raatikainen for age determination, and Emeritus Professor Pauli Bagge and Mr. Osmo Varis for assistance in larval seine netting. We are grateful also to Dr. Ian Winfield for checking the English language and for his valuable advice concerning the manuscript, together with that of two anonymous referees.

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